

contexts in which the stimuli occur [10].

Recent studies on humans support a parallel distinction, involving different roles for specific medial temporal lobe areas in recollection and familiarity [11]. Most studies on amnesia indicate that damage limited to the hippocampus results in selective deficits in recollection and relational memory, whereas the capacity to distinguish new and old items on the basis of familiarity is reported to be intact (but see [12,13]). Most functional imaging studies have also indicated that the hippocampus plays a selective role in recollection and relational memory, whereas the perirhinal cortex is activated during the presentation of novel items and decreasing activation levels signal familiarity. Other studies show that the parahippocampal cortex is activated during presentation of spatial scenes [14] or viewing of objects strongly associated with particular places [15], and this area is also activated during recollection of contextual information [16].

The new findings from Daselaar *et al.* [4] confirm and extend the evidence from earlier functional imaging studies. They confirm that (the posterior) part of the hippocampus is selectively involved in recollection, and the perirhinal and lateral entorhinal cortex is selectively activated by novel stimuli with progressively declining levels of activation for more familiar stimuli. The findings diverge from the literature in distinguishing the parahippocampal cortex and anterior hippocampus from the posterior hippocampus. However, the new data may be interpreted as a refinement, rather than a revision, of the functional divisions of the medial temporal lobe. Notably the direction of greater activation associated with stronger memory in the parahippocampal cortex and anterior hippocampus is the same as that in the posterior hippocampus, but the strength of activation is continuous in the former rather than all-or-none in the latter.

The methods of Daselaar *et al.* [4] have thus revealed differences

in the dynamics of memory retrieval in these components of the system. Other differences, indicated by the earlier studies, may also distinguish these areas. Thus, the continuous activation of the parahippocampal cortex may reflect the strength or amount of information in context signals [17]. And perhaps information processing in the anterior hippocampus reflects a more continuous retrieval of relational representations than that of the posterior hippocampus [18], and this difference may lead to a reconciliation of discrepant findings on the hippocampus [12,13]. Future efforts will confirm or deny these speculations. Meanwhile the new findings add to an emerging story about the functional organization of the medial temporal lobe memory system.

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Center for Memory and Brain, Boston University, Boston, Massachusetts 02215, USA.
E-mail: hbe@bu.edu

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Evolutionary Ecology: When Relatives Cannot Live Together

The importance of competition in determining species coexistence has been much debated. A phylogenetic analysis of sedges indicates that competitive exclusion may inhibit co-occurrence among closely related species, but not among more distant relatives.

T. Jonathan Davies

It is commonly accepted that there is a limit to the similarity of co-occurring species — the theory of 'limiting similarity' [1,2].

However, the deceptively simple question of how similar two species may be to each other before one competitively excludes the other has proven remarkably divisive [3,4]. One major obstacle

| Dominant ecological force | Functional traits | |
|---------------------------|-------------------|---------------|
| | Conserved | Convergent |
| Habitat filtering | Clustered | Overdispersed |
| Competitive exclusion | Overdispersed | Random |

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Figure 1. Predicted phylogenetic structure within a community under differing scenarios of functional trait evolution and alternative ecological determinants of co-occurrence. (Adapted from [6].)

to predicting when one species should displace another has been the difficulty in differentiating between the relative importance of two ecological forces: the fitness advantage a species gains by occupying a favourable habitat (habitat filtering), versus the cost of competition from species sharing similar resource requirements in that habitat (competitive exclusion). In the absence of competition, species with similar ecological requirements will have high fitness in similar environments. But as resources are divided among an increasing number of species, relative fitness will decline, potentially resulting in the displacement of the competitively inferior species. Phylogenetic methods offer a powerful approach for evaluating ecological patterns and, in particular, provide a robust null model for exploring the association between species distributions and ecological traits by controlling for the effects of shared ancestry [4–6].

Competitive exclusion and habitat selectivity may lead to phylogenetic structure in co-occurring species [6]. First,

co-occurring species may be more closely related to each other than expected from the regional species pool — phylogenetic clustering. Second, co-occurring species may be less closely related than expected — phylogenetic overdispersion. Whether one pattern comes to dominate over the other will depend upon the relative strengths of interspecific competition, habitat filtering and the evolutionary flexibility of functional traits determining fit to the environment (Figure 1). If closely related species share similar functional traits, and the benefits in occupying a suitable habitat outweigh the potential increased cost of competing with close congeners, phylogenetic clumping is predicted. If the cost of competition is high, however, phylogenetic overdispersion may occur. Alternatively, if the traits determining habitat preference are evolutionary labile, such that more distantly related taxa share similar habitat preferences due to convergence, our predictions will change. Habitat filtering, in which species distributions are largely determined by their fit to the environment, will tend to result in phylogenetic overdispersion, whereas strong interspecific competition may remove any trend between phylogeny and co-occurrence.

In a recent paper, Slingsby and Verboom [7] combine information from phylogenetic trees with fine scale distribution data to test for phylogenetic structure in schoenoid sedges (family Cyperaceae) in the Cape of South Africa, a global biodiversity hotspot. The floristic diversity of the Cape rivals that of the wet tropics, comprising around 9,000 species [8]. Recent molecular

evidence along with the high frequency of rare endemics in the region indicate that much of the Cape's diversity is a product of rapid *in situ* diversification within a few lineages [8–11], resulting in a large pool of closely related species. Hence, understanding the geographical patterns of species richness within the Cape requires an understanding of the mechanisms that govern species co-occurrence among closely related species, where the influence of common ancestry will be strongest.

Slingsby and Verboom [7] provide an elegant demonstration of phylogenetic overdispersion among the reticulate sheathed Tetraria, a monophyletic clade of Cape sedges. Using the evolutionary distance between species pairs from a molecular phylogenetic tree of sedges, the authors show that closely related sedges are less likely to co-occur than expected by chance, with phylogenetic relatedness setting an upper bound to co-occurrence (Figure 2). They also find greater than expected divergence in functional traits among co-occurring species. Because these traits were found to be evolutionary conserved, so that closely related Tetraria sedges are ecologically similar, Slingsby and Verboom [7] suggest the most parsimonious interpretation is that competitive exclusion, rather than habitat filtering, determines species co-occurrence within this clade.

It is of interest that, when comparisons are extended to across all Cape schoenoid sedges, the pattern breaks down, suggesting phylogenetic scale sensitivity to the processes regulating species co-occurrence. Moreover, at even higher taxonomic levels, previous studies found evidence for phylogenetic clustering [12]. One explanation for variation with phylogenetic scale would be greater niche conservatism in higher taxa, for example, if the traits defining the fundamental niche of a taxon were relatively invariable. Slingsby and Verboom [7] propose that the absence of evidence for increased trait conservatism at broader taxonomic levels within the sedges

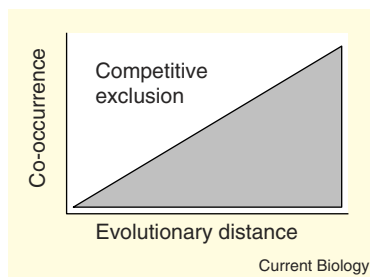


Figure 2. Expected relationship between co-occurrence and evolutionary distance (relatedness) assuming close relatives share similar traits (functional trait conservatism).

The grey area indicates potential for co-occurrence.

might imply that these traits are more important in terms of competitive interactions rather than habitat preferences. As evolutionary distance increases, species are likely to vary in an increasing number of traits, reducing the strength of competitive interactions. Therefore, competitive exclusion among close relatives would not preclude the possibility that habitat filtering influences community structure at broader taxonomic scales, but the important traits may differ.

How does this new study enhance our understanding of Cape diversity? Strong competition among closely related species in a region such as the Cape, where the species pool is composed of many close relatives, will place limits on species richness, as local richness is restricted by competitive exclusion. This same mechanism, by forcing spatial divergence of closely related species, will also result in high turnover of species along spatial gradients. As Slingsby and Verboom [7] observe, this rather neatly fits with the observation that the high diversity in the Cape is best characterised in terms of exceptional beta diversity (species turnover), whilst alpha diversity (local species richness) remains similar to that found in other Mediterranean-type biomes [9,10]. However, reasons for the rapid rates of diversification observed in

Cape lineages, such as the sedges, remain a matter for speculation. Might the same processes responsible for structuring ecological communities also drive speciation rates [13]?

Slingsby and Verboom [7] present a convincing argument for phylogenetic structure in community membership, a likely product of competitive displacement of closely related species sharing similar functional traits. Measuring the maximum evolutionary distance between co-occurring species on a phylogenetic tree can therefore provide an estimate of limiting similarity. However, the web of competitive interactions is likely to be complex within any natural community. Considering only pair-wise interactions will tend to underestimate competitive load. For example, if the strength of competition scales with relatedness, a species co-occurring with a single close relative might experience the equivalent competitive pressure as a species co-occurring with two more-distant relatives, yet pair-wise comparisons will suggest the competitive load of the latter to be half that of the former. Generating a comprehensive model of species-co-occurrence will be challenging, requiring knowledge of phylogeny, biogeography, and ecomorphology for all species within a community.

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Department of Biology, Gilmer Hall,
University of Virginia, Charlottesville,
Virginia 22904, USA.
E-mail: jdavies@virginia.edu

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Evolutionary Biology: How Did the Human Species Form?

A recent analysis has shown that divergence between human and chimpanzee varies greatly across the genome. Although this is consistent with 'hybridisation' between the diverging human and chimp lineages, such observations can be explained more simply by the null model of allopatric speciation.

N.H. Barton

Neutral DNA sequences accumulate mutations at a roughly constant rate. Thus, by comparing sequences from different species, we can estimate how long ago

these sequences diverged. The degree of divergence varies along the genome, primarily because the time when two lineages met in a common ancestor is a matter of chance [1,2]. In a recent paper, Patterson *et al.* [3] analyse a large

dataset — almost 30 megabases of aligned sequence from several primate species — and confirm earlier findings (for example [4,5]) that the divergence time between human and chimpanzee varies widely across the genome. They argue that this variation implies that there was hybridisation between the diverging lineages that ultimately led to humans and chimpanzees, and that some genes were exchanged between them much more recently than were other genes. While this kind of analysis of divergence across the whole genome promises to tell us much about the process of